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Differential pollinator response underlies plant reproductive resilience after fires

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Running tittle: Postfire pollination resilience

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Abstract

Background and aims Assessing the resilience of plant-animal interactions is critical to understanding how plant communities respond to habitat disturbances. Most ecosystems experience some level of natural disturbance (e. g., wildfires) to which many organisms are adapted to. Wildfires have structured biotic communities for millennia; however, the effects of fire on interactions such as pollination have only recently received attention. A few studies have shown that generalist plants can buffer the impact of fires by pollinator replacement, suggesting that the resilience to disturbance could depend on the level of specialization of the interactions. Here, we hypothesize that i) fires could impose negative effects on plants with specialized pollination systems, and ii) in large wildfires, these negative effects will be stronger with increasing distance inside the burnt because pollinators will need more time to recolonize.

Methods These questions were tested in the specialized pollination system of a widespread Mediterranean palm, *Chamaerops humilis*. The postfire pollination resilience was assessed in replicated wildfires representing three postfire ages by measuring the abundance of beetle pollinators and by estimating fruit set (i.e., proportion of flowers setting fruits) in burnt and unburned areas. To test for distance effects, plants were sampled along transects inside the burnt.

Key results This study revealed that despite a marked postfire decline in the specialist pollinator, exacerbated by the distance from the fire's edge, the palm's fruit set was barely affected. The temporary replacement by a sap beetle at burnt sites - an effective pollinator that had not been previously recognized - provided postfire reproductive resilience.

Conclusions The study shows that differential pollinator responses to disturbance can ensure plant success even in plants with only two functionally similar pollinators. This highlights the

1 importance of pollinator replacement and dynamics for the resilience of interactions and
2 ultimately of plant reproduction in disturbance-prone ecosystems.
3
4 **Keywords:** Arecaceae, *Chamaerops humilis*, *Derelomus chamaeropis*, entomophily, fire-prone
5 ecosystems, interaction resilience, *Meligethinus pallidulus*, palm, pollinator replacement, sap
6 beetle, weevil, wildfires.

INTRODUCTION

One of the main challenges in community ecology is to get a better understanding of how plant-animal interactions respond to disturbance. Specifically, mutualistic interactions like pollination play an essential role in the maintenance of biodiversity (Herrera and Pellmyr, 2002). There is evidence of negative impacts on plant fitness by the disruption of pollination interactions linked to recent human-induced disturbances such as habitat fragmentation (Aguilar *et al*., 2006), pesticides (Stanley *et al*., 2015) or species invasions (Chittka and Schürkens, 2001; Traveset and Richardson, 2006). In a broader temporal scale, most ecosystems have experienced some level of natural disturbance to which many organisms are adapted (Elmqvist *et al*., 2003). Assessing the effects of natural disturbances (e.g., wildfires) on pollination interactions may contribute to understand their resilience, which is important in the current context of increasing anthropogenic perturbations.

Wildfires are common natural disturbances that have shaped communities for millennia (Pausas and Keeley, 2009), resulting in the evolution of numerous adaptive traits and strategies that allow plants and animals from fire-prone regions to succeed under different fire regimes (Schütz *et al*., 1999; Keeley *et al*., 2011; He *et al*., 2012; Castellanos *et al*., 2015; Pausas and Parr, 2018). Despite this long fire history in many terrestrial ecosystems, the way in which pollination interactions cope with fire has only recently received attention (Dafni *et al*., 2012; Brown *et al*., 2017), and most research on this topic has been focused on pollination by bees (Ne'eman *et al*., 2000; Potts *et al*., 2001; Moretti *et al*., 2006; Lazarina *et al*., 2016). Assessing the effects of fires on plant pollination is especially relevant given the current anthropogenic-driven disruptions of the natural fire regimes in different regions.

Fires affect plant and pollinator communities as well as their interactions (Potts *et al*., 2003; Lazarina *et al*., 2016; Ponisio *et al*., 2016). The time since the last fire (postfire age) shapes the pollinator community because it alters vegetation structure, floral rewards and the pollinator's access to bare ground and nesting places (Pauw, 2007; Moretti *et al*., 2009). During the first year after a fire, if the vegetation recovery is rapid, an increase in nesting sites and floral resources provided by fire-stimulated plants, via resprouting or germination from the seed bank, can attract many pollinators into the burnt area. However, if postfire recovery is slow, low availability of water and food resources (DeBano and Conrad, 1978) can delay pollinator recolonization. This can be accentuated if pollinators are highly sensitive to fires (i.e., they do not survive, escape, or move to unburned refugia). In such cases, recently burnt areas would continue to have low pollinator richness and abundance, resulting in low levels of plant reproduction (Ne'eman and Dafni, 1999; Ne'eman *et al*., 2000). Postfire age can also interact with ecological and functional traits of pollinators, such as niche specialization, body size, or life cycle, leading to differences in ability to recolonize after fire (Bradstock *et al*., 2002; Moretti *et al*., 2006). In addition, other factors characterizing the fire regime such as fire intensity and frequency may affect the postfire succession and ultimately pollinator responses.

For plant species with generalized pollination systems (i.e., a diverse set of floral visitors that are effective pollinators) the negative impact of fires can potentially be buffered if pollinators respond differently to fire (Bond, 1994; Potts *et al.*, 2001; Pauw, 2007), as shown by studies on different disturbances (Ashworth *et al.*, 2004; Aguirre and Dirzo, 2008; Hallett *et al*., 2017). This is consistent with theoretical predictions of the advantages of generalized pollination (Waser *et al*., 1996), and could be explained, for example, if the different pollinators belong to a variety of functional groups that are differentially affected by disturbance (referred to as

"response diversity"; Ives *et al*., 1999; Walker *et al*., 1999; Bartomeus *et al*., 2013). However, fires can have stronger effects on plants with specialized interactions as we have previously shown for seed predation (García *et al*., 2016). For plants that rely on one or a few species of pollinators for reproduction, the loss of their interacting partners after fires will trigger a decrease in plant reproductive success, at least until the interaction is recovered. That is, for these plant species, the vulnerability to fire may be related to the resilience (i.e., the capacity of a system to maintain its function and identity after a change) of their mutualistic interactions. A variety of responses by pollinators with different nesting preferences or by plants and pollinators varying in their dispersal abilities may provide resilience to pollination systems under disturbance.

We hypothesize that plant species with specialized pollination systems will be negatively affected by fires due to impacts on their few pollinators that in turn affect the plant's reproduction. To test our hypothesis we used the pollination system of the dwarf palm *Chamaerops humilis* (Arecaceae). The current knowledge indicates that this dioecious palm is exclusively pollinated by the nursery weevil *Derelomus chamaeropis* (Curculionidae; Anstett, 1999; Dufaÿ and Anstett, 2004). The weevil feeds and develops inside persistent old palm inflorescences, which are burnt during fires and thus a strong decrease in pollinator abundance in burnt areas is expected. In addition to *D. chamaeropis*, small sap beetles (Nitidulidae) are also visitors of the palm's inflorescences (Anstett, 1999, per. obs.). Because sap beetles are important pollinators of other palm species (Henderson, 1986; Anderson *et al*., 1988; Aguirre and Dirzo, 2008; Barfod *et al*., 2011), we also predict that *Meligethinus pallidulus* (Nitidulidae) could contribute to the pollination of *C. humilis*. In addition, the strength of the interactions can vary along the distance inside the burnt area while recolonization takes place, as has been shown for herbivory and seed predation in large wildfires (Knight and Holt, 2005; García et al., 2016). This

may lead to stronger postfire effects on pollinator abundance and fruit set levels with increased distance inside the burnt.

In summary, we study the resilience of *C. humilis* pollination to wildfires by comparing the abundance of pollinators on the palm's inflorescences, and their consequences for fruit set, in burnt and in unburnt (paired) sites with different postfire ages. We also test whether the effects of fire on the two beetle pollinators and on palm fruit set are stronger with increasing distance from the fire's edge.

MATERIAL AND METHODS

Study system

The Mediterranean dwarf palm *Chamaerops humilis* is a small dioecious palm native to the coastal shrublands of the western Mediterranean Basin. The plant resprouts quickly after fires and produces flowers the following spring (Paula *et al*., 2009). With or without fire, flowering occurs in early spring, with male anthesis starting one or two weeks before female anthesis (Anstett, 1999). Although *C. humilis* can occasionally show polygamous individuals, we did not observe functional hermaphroditic flowers in the studied populations. New yellow-greenish inflorescences emerge from the palm trunks while old brown inflorescences remain for years. Male and female individuals have branched inflorescences enclosed by two bracts (prophyll) that gradually opens during flowering. Female flowers have three free carpels and develop into a polydrupe with 1-3 drupes. Each drupe was considered as a fruit as it acts as the dispersal unit containing the seeds.

C. humilis has a specialized nursery pollination system involving the weevil *Derelomus chamaeropis* (Curculionidae; Anstett, 1999). During the winter, weevil larvae develop from eggs

laid the previous spring inside the rachis of persistent old inflorescences (Dufaÿ and Anstett, 2004; Jácome-Flores *et al*., 2018). Adult *D. chamaeropis* (mean body length 2.9 ± 0.4 mm, excluding the rostrum, n= 6) emerge in early spring and are attracted to flowering plants by a chemical signal emitted by leaves during the flowering season (Dufaÿ *et al*., 2003). Female and male leaves produce a similar odour preventing the weevil from avoiding female palms, although the insect shows preference for male individuals, where it feeds on pollen (Dufaÿ *et al*., 2003; Dufaÿ *et al*., 2004; Jácome-Flores *et al*., 2018).

Our field observations suggest that there is another common visitor on *C. humilis* inflorescences, the sap beetle *M. pallidulus* (Nitidulidae, mean length 1.7 ± 0.2 mm, n= 6) although its role on the palm's pollination is unknown. Occasionally honey bees visit male inflorescences but we have never seen them on female flowers and thus do not consider them as potential pollinators. Ants are erratic and infrequent visitors and also unlikely to pollinate this dioecious plant. There have been suggestions that wind could also play a role in pollination of *C. humilis* (Herrera, 1989; Jácome-Flores *et al*., 2016). Although most previous evidence does not support this possibility (Anstett, 1999; Dufaÿ and Anstett, 2004), we experimentally test it here (see results).

Study areas

The study was carried out during 2016 and 2017 in four burnt sites in Eastern Spain after wildfires (Table 1 and Fig. 1 for details). Two sites (Dénia and Tivissa) were studied in both 2016 and 2017, and two other sites (Xàbia and Carcaixent) were studied in 2017 only. This design involved replicated sampling of sites during 1, 2 and 3 years postfire (Table 1). All sites are located in coastal Mediterranean shrublands dominated by *Cistus monspeliensis* and *C.*

albidus (Cistaceae) and Fabaceae species such as *Calicotome spinosa* and *Ulex parviflorus*. All fires were typical Mediterranean crown fires (Keeley *et al.*, 2012), that is, of high intensity and fully affecting most plants (little unburned islands, see Fig. 1).

Pollinator exclusion experiment: the role of the different pollinators

To investigate the role of *M. pallidulus* in *C. humilis* pollination and rule out the possible contribution of wind, we conducted a pollinator exclusion experiment during the flowering peak of *C. humilis* in 2017. We selected 12 female *C. humilis* plants from natural unburned populations in Dénia. We chose four undehisced inflorescences per plant (in 1 or 2 stems) and assigned one inflorescence to each of four pollination treatments in which the inflorescences were either enclosed in mesh bags of different pore diameters or left as an unbagged open control. All bags were tied to the stems and the aperture sealed with silicone. We also added silicone to the base of inflorescences in the control treatment to control for possible effects of the experimental manipulation. The four treatments were: i) pollination exclusion using a paper bag to exclude both wind and insect pollination; ii) potential wind pollination by enclosing the inflorescence in a bag with pore diameter 0.15 mm; iii) potential wind and small-insect (i.e., *M. pallidulus*) pollination, by enclosing the inflorescence in a bag with pore diameter 1.10 mm; and iv) unbagged control, in which wind, *M. pallidulus* and *D. chamaeropis* were able to pollinate.

We used the palm's fruit set as an estimate of female reproductive success by counting the flowers and fruits for each inflorescence in late June. We bagged the inflorescences and collected the fruits on the same day for all plants across treatments. We estimated the fruit set as the number of drupes produced in relation to the total potential drupes (i.e., the total number of flowers in the inflorescence multiplied by three carpels). For this, we collected all sampled

inflorescences and counted all drupes produced and the scars left by aborted flowers on the inflorescence rachis. The number of flower scars is a good estimator of the potential fruit production (Pearson correlation between number of flowers in fully open inflorescences and flower scars in the same inflorescences was 0.95, $P<0.001$, n= 262, tested in plants from burnt and unburned areas during the sampling of the palm's fruit set, see below).

To test the effectiveness of the bags used for excluding the flow of airborne pollen (treatments ii and iii), we performed an additional experiment using the common anemophilous grass *Hyparrhenia hirta*. This species has hermaphroditic and staminate flowers with pollen grains of similar size (diameter 28.20 ± 1.82 µm, n= 10) to *C. humilis* pollen (diameter 20.45 ± 1.53 µm, n= 10). We bagged non-flowering shoots of ten *H. hirta* plants using one bag of both mesh size per plant. These shoots were surrounded by other flowering individuals of *H. hirta*, but were not directly touching any other flowers. Each bag contained two adhesive strips (1 cm^2) to retain wind-dispersed pollen grains that entered the bag. After one week we dyed the adhesive strips with fuchsine jelly (Beattie, 1972). We counted any pollen grain observed with the ImageJ software (Rasband, 2007). The results suggested that bags of the wind pollination treatment did not reduce the amount of wind dispersed pollen (mean number of grains/adhesive strip: 186 ± 98 in 1.10 mm pore bags vs. 204 +115 in 0.15 mm pore bags, GLM with Poisson error distribution: estimate=0.040± 0.033, z-value=1.209, $P = 0.22$, n= 10 bags of each pore size), and thus the bags used were appropriate for the experiment.

Insect pollen loads

To test for differences in the numbers of pollen grains carried by *M. pallidulus* and *D. chamaeropis*, we haphazardly captured one individual of each species from each of 20 flowering

C. humilis plants (ten per sex) at each study site in 2017. We individually kept the insects in Eppendorf tubes at -20^{0}C until a sample of the pollen loads was collected from the whole body surface of each individual using fuchsine jelly cubes. We melted the cubes on microscope slides and then identified the pollen loads from insects collected on female palms by comparing with a reference pollen library constructed by collecting anthers of *C. humilis* and 12 co-flowering plant species from the study sites. We dyed the pollen grains of each plant species with fuchsine jelly and identified under a microscope (Leica DMR). To measure pollen size (of *C. humilis* and the co-flowering plant species) for the reference pollen library and count the number of *C. humilis* grains carried by the insects we used the ImageJ software (Rasband, 2007) with a specific script developed for the counting analysis.

Postfire changes in pollinators and fruit set

To study postfire changes in pollinators and fruit set at each site, we tagged palms within the perimeter of the burnt area and in adjacent unburned (control) areas with conditions (soil type, topography, and plant species composition) similar to those within the burnt area prior to the fire. Burnt and adjacent unburned areas were embedded in the same vegetation matrix type (shrublands). We performed all sampling in mid-April at the peak of anthesis of male plants, and the beginning of female flowering. In each burnt and unburned area, we sampled 98-197 *C. humilis* plants of both sexes separated from each other by at least 5m. To test the effects of the distance from the edge on pollinator abundance and palm fruit set, plants were sampled along transects (of ca. 30 to 700 m) from the fire's edge to the interior (Fig. 1). We sampled and georeferenced a total of 744 plants in 2016 and 796 in 2017 (n= 1540 plants). At burnt areas, transects allowed us to investigate the effect of distance from the edge of the fire on the two

beetles abundance and on the palm's fruit set; this distance was computed from the geographical coordinates with Quantum GIS v. 2.8 (Quantum GIS Team, 2013) software.

For each male plant, we counted the number of inflorescences and, in one inflorescence at anthesis, the abundance of *D. chamaeropis* and the presence (2016) or number (2017) of *M. pallidulus* individuals during three-minute censuses. When part of the male inflorescence was not completely outside the prophyll, we carefully opened the prophyll to count all beetles. The insects are easily detected at the base of inflorescences, moving around the bracts that enclose them. We conducted the pollinator censuses between 9:30 and 16:00h on sunny days with similar weather conditions across all sites. To assess whether the maturity of *C. humilis* inflorescences differed between burnt and control areas in a way that could affect other analyses, we classified the phenological stage of each sampled male inflorescence as either: 1) Beginning of anthesis (many closed anthers and small amounts of pollen); 2) Anthesis (yellow flowers producing pollen); and 3) End of anthesis (flowers turning brown with small amounts of pollen present). For female plants we counted the total number of inflorescences and tagged one of them (at anthesis) to estimate fruit set later in the season (see below). The number of *D. chamaeropis* and *M. pallidulus* on female inflorescences was also recorded during three minutes. Then we classified the phenological stage of the female inflorescence as Closed (including partially-open inflorescences); or Open (inflorescences with only their lowest part inside the prophyll). We estimated the fruit set in late June, when fruits were developing, in all tagged inflorescences and by using the same methodology as described in the pollinator exclusion experiment.

Statistical analysis

We investigated the effects of the three pollination exclusion treatments and control treatment on palm fruit set (proportion of drupes in relation to potential drupes) as response variable using a Generalized Linear Models (GLM) with a quasi-binomial error distribution to control for overdispersion and the logit link function in *stats* package in R (R Core Team, 2017). Pollination treatment was included as predictor variable and the number of experimental stems per plant (one or two) as a covariate. We then tested for differences in pollination treatments by post-hoc pairwise comparisons adjusted by Bonferroni's correction for multiple tests with the *multcomp* package in R (Hothorn *et al*., 2008). To explore potential differences in the pollen loads carried by *D. chamaeropis* and *M. pallidus* we fitted a GLM with number of pollen grains (with Poisson error distribution) as the response variable and insect species, plant sex and their interaction as predictors.

To test the effect of fire on *D. chamaeropis* abundance on *C. humilis* we used a GLM with a negative binomial distribution and a log link function. We included as predictor variables fire treatment (unburned versus burnt), number of inflorescences per plant, plant sex, site, and the interaction between fire treatment and site. To analyze the effect of distance from the edge of the fire on *D. chamaeropis* abundance, we ran a similar GLM in which the distance of each plant from the fire edge was included as a predictor variable. Only plants inside the burnt areas (n= 354 in 2016 and n= 401 in 2017) were included in the distance model; and interactions that did not contribute significantly were removed from the final model. To test whether the effect of distance to the edge varied when consider the postfire age categories, an additional GLM grouping the sites by postfire age (1 year vs 3 years postfire) was also fitted.

We ran equivalent models for *M. pallidulus* abundance on the plant in 2017. To test for differences in the presence of *M. pallidulus* beetles on *C. humilis* plants in 2016, when only

presence data were available, we used GLMs with a binomial error distribution (presence vs absence) and a logit link function. For *M. pallidulus* presence, the fire and distance from the edge models both included the same predictor variables and sample sizes as the abundance models.

Before analyzing fruit set data, we checked for differences in the proportions of the developmental stages of inflorescences in our samples from the burnt and unburned areas. No differences were detected in male (X^2= 1.83, df= 2, P = 0.40, n= 808 plants) or female inflorescences (X^2= 0.41, df= 1, P= 0.55, n= 732 plants).

To test whether fire affected *C. humilis* fruit set, we used a GLMM with a binomial error distribution and a logit link function. To account for overdispersion we included an observation-level random effect (Harrison, 2015) by running a GLMM with individual plant as random factor using the *lme4* package in R (Bates *et al*., 2015). We included as fixed factors fire treatment (unburned versus burnt), site and their interaction. We added the number of female inflorescences as a covariate in the model after checking its independence from the predictors. To test whether these models were congruent with the three postfire age categories, we ran additional GLMM models of the effects of fire on fruit set where sites were grouped by postfire age (1, 2 and 3 years postfire, with plant and site as random factors).

To investigate the response of *C. humilis* fruit set to the distance from the fire's edge we ran a GLMM with female plants from burnt areas. We included the distance of each plant from the fire's edge and site as fixed effects, new produced inflorescences as a covariate, and plant as random factor.

Because of the differences in the number of studied sites (two in 2016 and four in 2017), we fitted fire (unburned vs burnt) and distance models separated for each sampling year. Prior to model fitting, the two continuous predictors, distance inside the burnt areas and number of

inflorescences were mean-centered. To test for differences of fire treatment (burnt vs unburned) among the study sites (in all models with a significant interaction term), we conducted post-hoc pairwise comparison for multiple test as described above (Bonferroni's adjusted). All analyses and graphics were performed in R software version 3.4.2 (R Core Team, 2017).

RESULTS

Pollination exclusion experiment

The pollinator exclusion experiment confirmed that *C. humilis* is exclusively insect-pollinated, that is, wind is not involved on its pollination (see also Jácome-Flores 2015). Inflorescences from the open controls produced a 12.15% higher fruit set (28.30 ± 7.61 % mean fruit set, n= 12 plants) than any bagged treatment (Fig. 2, $P < 0.01$ in all comparisons, see Supplementary Data Table S1 for details). In addition, *C. humilis* inflorescences from the wind and small-insect pollination treatment showed a higher fruit set (16.15 ± 10.41 % mean fruit set, n= 12 plants) than those in the wind pollination (1.19 ± 2.32 % mean fruit set, $P < 0.001$, n= 12 plants, Fig. 2) and pollination exclusion treatments (0.87 ± 0.75 % mean fruit set, $P < 0.001$, n=12 plants, Fig. 2). No significant differences were observed between inflorescences with wind pollination only and complete pollination exclusion bags ($P = 0.95$, n= 12 plants, Fig. 2, Supplementary Data Table S1). The number of sampled stems (one or two) did not affect the palm fruit set (estimate= 0.155 ± 0.224, t-value= 0.691 $P = 0.49$, n= 12 plants).

Insect pollen loads

Both *D. chamaeropis* and *M. pallidulus* carried pollen from *C. humilis* male plants to female plants (Fig. 3). Only a very small proportion of the pollen transported to female inflorescences

was not from *C. humilis* (0.86 % of that on *D. chamaeropis* and 1.54 % of that on *M. pallidulus*). Insects collected at male inflorescences were carrying more grains than insects from female inflorescences (for *D. chamaeropis*: 4180 ± 2041.4 vs 826 ± 207.6 mean grains/individual; for *M. pallidulus*: 803 ± 202.1 vs 387 ± 91.2, estimate = 0.729 ± 0.007, z-value= 103.1, $P < 0.001$, n= 80 individuals per insect species, Supplementary Data Fig S.1). *D. chamaeropis* carried more pollen grains than *M. pallidus* on both male and female inflorescences (estimate= 0.760 ± 0.007, z-value= 106.2, $P < 0.001$ n= 80, Supplementary Data Fig. S1).

Postfire changes in pollinators and fruit set

Burnt areas showed a marked reduction in *D. chamaeropis* abundance compared with unburned areas, and the weevil was almost absent in the first and second year postfire (88% and 74% average reduction, respectively; Fig. 4). Weevil numbers were significantly lower inside the burnt areas in the two most recently burnt sites (Xàbia and Carcaixent), and in Tivissa two and three years after the fire (Fig. 4, Table 2; see Supplementary Data Tables S2 and S3). Male plants had more weevils than female plants, both outside and inside the burnt areas (mean number of weevils/male inflorescence=4.70 ± 5.93 at controls vs 1.85 ± 3.12 at burnt areas, and 0.95 ± 1.67 at controls vs 0.58 ± 1.34 weevils/female inflorescence at burnt areas; n=808 males and n=732 females; Table 2). Plants from burnt sites in 2017 showed a negative relationship between weevil abundance and distance from the fire's edge (P <0.001, Table 2 and Supplementary Data Table S3 for full details). However, the posterior model grouping of the sites by postfire age (1 year vs 3 years postfire) revealed that this effect occurred only in palms from recently burnt sites (interaction between distance and 1-year postfire age, estimate= -0.009± 0.002, t-value= -4.25, $P < 0.001$, n=401 plants at Xàbia and Carcaixent sites, Fig. 5).

Burnt and control areas showed similar numbers of *C. humilis* plants with *M. pallidulus* beetles (46.7% in burnt and 51.4% in unburned areas). For 2017 (the year with quantitative data for both insect species), the number of *M. pallidulus* individuals per inflorescence was also similar after the fires (Unburned vs Burnt: $P = 0.33$, n= 796 plants, Supplementary Data Table S3 and Fig. S2). That is, neither fire nor distance effects were detected on the sap beetle's abundance on *C. humilis* plants in 2017, nor on its presence in 2016 (Table 2, Supplementary Data Tables S2 and S3 for statistic values).

Despite lower *D. chamaeropis* abundance, fruit set decreased only in the recently burnt Xàbia and, to a less extent, in Tivissa two years after the fire (Fig. 6, Table 2, Supplementary Data Table S4 for details). We did not detect significant differences in fruit set three years after the fires, or any effect of distance from the fire's edge (Fig. 6, Table 2, Supplementary Data Tables S2 and S3 for statistic values). The GLMM models on the effects of fire on fruit set in which sites were grouped by postfire age also showed that fruit set was only negatively affected 1 year postfire (Unburned vs Burnt: estimate =0.72 ±0.175, *z*-value= 4.16, $P < 0.001$, n=196 plants).

DISCUSSION

Our study highlights the importance of pollinator replacement as a way of providing resilience to disturbance in plant-pollinator interactions, even in a plant with a limited number of pollinators. Although we recorded a marked decline in numbers of the weevil pollinator after fires, *C. humilis* fruit set was barely affected. A temporary replacement by the sap beetle *M. pallidulus*, an effective pollinator that has not been previously recognized as such (Herrera, 1989; Anstett, 1999; Dufaÿ and Anstett, 2004), explains the fast recovery. The abundance of this beetle was

unaffected by the fires and provided resilience to the pollination process. As a result, fires did not alter the palm's reproduction in most study sites and fruit set showed a complete recovery in only three years.

In unburned conditions, visits by the sap beetle *M. pallidulus* produced a mean 16.15% fruit set compared to 28.30% in the controls also visited by *D. chamaeropis*. Differences between these two treatments are probably explained by the higher amount of pollen carried by *D. chamaeropis*. This is consistent with the known importance of the weevil as pollinator (Anstett, 1999; Dufaÿ and Anstett, 2004), although further research is needed to evaluate the possible differences in pollination efficiency between the two species. Contrary to the unburned areas, our study suggests that at the most recently burnt sites (where the weevil was virtually absent), *C. humilis* pollination relies on the sap beetle (which was not affected by fire), and this replacement may last until the weevil recolonizes the burnt sites. In addition, pollen loads of both insects consisted mainly of *C. humilis*, suggesting a marked specialization (at least while the plant is flowering) which may avoid potentially negative effects of heterospecific pollen deposition (Thomson *et al*., 1982; Ashman and Arceo-Gómez, 2013).

Fires had contrasting effects on the presence and abundance of the two beetle species, with a stronger negative effect on *D. chamaeropis* compared to *M. pallidulus.* This striking weevil decline is consistent with earlier evidence on the negative effects of wildfires on other weevil species from temperate zones (Moretti *et al*., 2004). The life cycle of *D. chamaeropis* is completely dependent on old dry *C. humilis* inflorescences, within which female individuals lay their eggs and the weevil develops (Anstett, 1999; Dufaÿ and Anstett, 2004). Most old inflorescences burn in wildfires, and we did not detect any *D. chamaeropis* larvae in a preliminary sampling of the palm immediately after fire (unpublished data). Experimental tests

on a similar interaction between butterflies and cycads have shown that fire temperatures can kill all pupae growing inside fronds of the host plants (Thom *et al*., 2015). In all such cases, the burnt area must be recolonized from surrounding populations, which can result in spatial gradients in insect abundance and in turn in their interactions inside the burnt (Knight and Holt, 2005). Consistently, we observed a significant decline in weevil abundance on *C. humilis* plants with increasing distance to the edge of the burnt area in the first postfire year, followed over the years by an increase in the number of weevils in the depleted parts of the burnt area.

Meligethinus pallidulus also appears to be specialized on *C. humilis* pollen at least during the plant's flowering season. Little is known about the biology of this sap beetle, but its life cycle is likely to depend on *C. humilis* (Ponel and Lemaire, 2012; Audisio *et al*., 2014). We have not detected any *M. pallidulus* larvae inside the palm´s inflorescence: an examination of complete old inflorescences from 180 male plants at three sites only revealed the presence of *D. chamaeropis* and some Lepidoptera (data not shown). There are three possible explanations for the rapid postfire recovery of *M. pallidulus*. First, *M. pallidulus* larvae may develop inside the palm´s stem. Adults are often seen inside the stems (Supplementary Data Fig. S3) where they could survive fires thanks to the protection by the fibrous bark-like structure (e.g., Brennan *et al*., 2011). The second possible explanation is that the higher densities of *M. pallidulus* on the plant, compared to the weevil in the unburned sites, may allow faster recolonization. This is consistent with a previous study where high numbers of sap beetles contributed to ensure a tropical palm fruit set even in highly fragmented zones (Aguirre and Dirzo, 2008). Finally, larger dispersal distances by the sap beetle might also be a mechanism explaining its fast recolonization from the surrounding areas (Saint-Germain et al., 2004). Further studies are needed to determine whether either of these routes to postfire recovery is driving the sap beetle's response. In any case, the

fast recovery of *M. pallidulus* appears to maintain *C. humilis* pollination after fires. This, together with quick resprouting by the palm (Paula *et al*., 2009), and its ability to flower in the spring following a fire contribute to the high success of the palm in fire-prone environments. In addition, the quick availability of fruits at burnt sites may have broader implications for ecosystem resilience, like maintaining frugivorous vertebrates and accelerating the postfire recolonization of plants in fire-prone landscapes. Fruit dispersers such as badgers, foxes and deer can also transport seeds of other species (Herrera, 1989; Fedriani and Delibes, 2011; Castañeda *et al*., 2017) from the surrounding areas, which ultimately may promote the arrival of seeds in freshly burnt sites.

However, fire did decrease palm fruit set in two sites. This reduction in the Xàbia site during the first postfire year could be related to the marked significant reduction in the weevil abundance together with the low numbers of the sap beetles (although no significant) at the burnt area (Table 2, Supplementary Data Fig. S2). In Tivissa two years after the fire, weevil abundance was very low; *M. pallidulus* was present but we lack information on its abundance and thus we cannot fully explain the reduction of fruit set in this case. Abiotic factors not measured here, such as soil nutrient and water availability, could also alter the plant reproductive success after fire (Carbone and Aguilar, 2017) and explain some of this variation. While fire may reduce *C. humilis* fruit set in some instances, this is not a general outcome, and only three years after the fires effects on fruit set were no longer detectable.

The frequent asymmetric nature of plant-pollinator interactions (specialist species interact with generalist ones) provides resilience to disturbance (Ashworth *et al*., 2004; Vázquez and Aizen, 2004). This has led to the prediction that disturbances will have strong consequences on symmetric pollination interactions because of the reciprocal dependence between the mutualistic

partners. However, empirical studies assessing the reproductive costs of disturbance for plants engaged in obligated pollination systems are still scarce (Bronstein and Hossaert-McKey, 1995; Lemke and Porembski, 2013; Suchan *et al.*, 2015). Some of these studies have shown that these highly specialized interactions can be also resilient if the species involved have traits that confer a rapid ability to respond (Bronstein and Hossaert-McKey, 1995) or if the plant has additional (but overlooked) non-nursery pollinators at disturbed areas as we show here (Suchan *et al*., 2015).

This resilience could be more frequent in specialized interactions from disturbance-prone environments, like fire-prone ecosystems, as plants and animals in these areas have evolved persistent traits under recurrent disturbances (Schütz *et al*., 1999; Keeley *et al*., 2011; He *et al*., 2012; Castellanos *et al*., 2015; Pausas and Parr, 2018). Yet only a few studies have assessed the effects of fire on specialized pollination interactions. For instance, the higher seed set levels at early postfire ages in fire-stimulated flowering orchids depended on specialist oil-collecting bees for reproduction (Pauw, 2007). In contrast, old fires were positively related to pollinator visitation in a specialist Australian orchid (Brown *et al*., 2016; Brown and York, 2017). These studies together with our results, support the view that different species reach a reproductive optimum at different postfire succession stages (Moretti *et al*., 2006, 2009; Lazarina *et al*., 2016). It is also noteworthy that other fire characteristics such as fire frequency or the diversity of fire histories at the landscape level ("pyrodiversity") can also alter the outcome of plant-pollinator interactions at different spatial scales (Brown *et al*., 2016; Ponisio *et al*., 2016; Brown and York 2017; Carbone and Aguilar, 2017). The success of highly specialized pollination systems in floras from different fire-prone regions (Gottsberger, 1986; Johnson and Steiner, 2003; Johnson, 2010) calls for further research on the idea that resilience is common in such environments.

CONCLUSIONS

The resilience of plant communities to face disturbances may rely, at least in part, on the ability of reorganizing their mutualistic interactions, which can offset the indirect negative effects on plant reproduction. Earlier works suggested that a high diversity of interacting species may ensure a generalist plant species' success under fluctuating environmental conditions (Albrecht *et al*., 2012; Bartomeus *et al*., 2013). Such high diversity may allow for pollinator replacement and thus the resilience of the reproduction after disturbance (Potts *et al*., 2001). Here we provide field evidence of an unexpected pollinator replacement after fire in a specialized pollination system. To what extent postfire pollination replacement is common in other specialized systems remains to be studied. Overall, the current fire regimes changes in many ecosystems call for further research on the effects of fire on the dynamics of plant-animal interaction assemblages and ultimately on the implications for plant reproduction. Only with this research we can really evaluate the impact of future fire regimes on biodiversity.

SUPPLEMENTARY DATA

Additional supporting information may be found in the online version of this article and consist of the following.

Table S1: Post-hoc pairwise comparisons of regression coefficients among pollinator exclusion treatments (the GLM also included the number of palm stems as a covariate) on *Chamaerops humilis* fruit set (response variable).

Tables S2: Detailed statistic results of the GLM and GLMM models of the effects of fire and distance from the fire's edge on the number of *Derelomus chamaeropis*, presence of *Meligethinus pallidulus* and *Chamaerops humilis* fruit set in 2016.

Tables S3: Detailed statistic results of the GLM and GLMM models of the effects of fire and distance from the fire's edge on the number of *Derelomus chamaeropis* and *Meligethinus pallidulus* and on *Chamaerops humilis* fruit set in 2017.

Table S4: Post-hoc pairwise comparisons of regression coefficients of the interaction between fire treatment (Unburned vs burnt) and study site from the models of fire effects on *Derelomus chamaeropis* abundance and *Chamaerops humilis* fruit set.

Figure S1: Number of *Chamaerops humilis* pollen grains carried per individual by the two pollinator species, *Derelomus chamaeropis* and *Meligethinus pallidulus*, on male (A) and female (B) *Chamaerops* inflorescences.

Figure S2: Number of *Meligethinus pallidulus* individuals per inflorescence at each study site in uburned and burnt areas at 2017 including 2 postfire ages.

Figure S3: *Meligethinus pallidulus* inside and outside the prophyll of a male inflorescence of *Chamaerops humilis* from one of the burnt areas.

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LITERATURE CITED

Aguilar R, Ashworth L, Galetto L, Aizen MA. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters* 9: 968–980.

Aguirre A, Dirzo R. 2008. Effects of fragmentation on pollinator abundance and fruit set of an abundant understory palm in a Mexican tropical forest. *Biological Conservation* 141: 375–384.

Albrecht M, Schmid B, Hautier Y, Müller CB. 2012. Diverse pollinator communities enhance plant reproductive success. *Proceedings of the Royal Society B* 279: 4845–4852.

Anderson AB, Overal WL, Henderson A. 1988. Pollination ecology of a forest-dominant palm (*Orbignya phalerata* Mart.) in northern Brazil. *Biotropica* 20: 192–205.

Anstett MC. 1999. An experimental study of the interaction between the dwarf palm (*Chamaerops humilis*) and its floral visitor *Derelomus chamaeropsis* throughout the life cycle of the weevil. *Acta Oecologica* 20: 551–558.

Ashman TL, Arceo-Gómez G. 2013. Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. *American Journal of Botany* 100: 1061–1070.

Ashworth L, Aguilar R, Galetto L, Aizen MA. 2004. Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *Journal of Ecology* 92: 717–719.

Audisio P, Cline AR, Solano E et al. 2014. A peculiar new genus and species of pollen-beetle (Coleoptera, Nitidulidae) from eastern Africa, with a molecular phylogeny of related Meligethinae. *Systematics and Biodiversity* 12: 77–91.

Barfod AS, Hagen M, Borchsenius F. 2011. Twenty-five years of progress in understanding pollination mechanisms in palms (Arecaceae). *Annals of Botany* 108: 1503–1516.

Bartomeus I, Park MG, Gibbs J, Danforth BN, Lakso AN, Winfree R. 2013. Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecology Letters* 16: 1331–1338.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.

Beattie AJ. 1972. A technique for the study of insect-borne pollen. *The Pan-Pacific Entomologis*t 47, 82.

Bond WJ. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions: Biological Sciences* 344: 83–90.

Bradstock RA, Williams JE, Gill MA. 2002. *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge: Cambridge University Press.

Brennan KE, Moir ML, Wittkuhn RS. 2011. Fire refugia: the mechanism governing animal survivorship within a highly flammable plant. *Austral Ecology* 36: 131–141.

Bronstein JL, Hossaert-McKey M. 1995. Hurricane Andrew and a Florida fig pollination mutualism: resilience of an obligate interaction. *Biotropica* 373–381.

Brown J, York A, Christie, F. 2016. Fire effects on pollination in a sexually deceptive orchid. *International Journal of Wildland Fire* 25: 888–895.

Brown J, York A. 2017. Fire, food and sexual deception in the neighbourhood of some Australian orchids. *Austral Ecology* 42: 468–478.

Brown J, York A. 2017. Fly and wasp diversity responds to elements of both the visible and invisible fire mosaic. *International Journal of Wildland Fire* 26: 434–443.

Brown J, York A, Christie F, McCarthy M. 2017. Effects of fire on pollinators and pollination. *Journal of Applied Ecology* 54: 313–322.

Carbone LM, Aguilar R. 2017. Fire frequency effects on soil and pollinators: what shapes sexual plant reproduction? *Plant Ecology* 218: 1283–1297.

Castañeda I, Fedriani JM, Delibes, M. 2017. Potential of red deer (*Cervus elaphus*) to disperse viable seeds by spitting them from the cud. *Mammalian Biology* 90: 89-91.

Castellanos MC, González-Martínez SC, Pausas JP. 2015. Field heritability of a plant adaptation to fire in heterogeneous landscapes. *Molecular Ecology* 24: 5633–5642.

Chittka L, Schürkens S. 2001. Successful invasion of a floral market. *Nature* 411: 653–653.

Dafni A, Izhaki I, Ne'eman G. 2012. The effect of fire on biotic interactions in Mediterranean basin ecosystems: pollination and seed dispersal. *Israel Journal of Ecology & Evolution* 58: 235–250.

DeBano LF, Conrad CE. 1978. The effect of fire on nutrients in a chaparral ecosystem. *Ecology* 59: 489–497.

Dufaÿ M, Anstett MC. 2004. Cheating is not always punished: killer female plants and pollination by deceit in the dwarf palm *Chamaerops humilis. Journal of Evolutionary Biology* 17: 862–8.

Dufaÿ M, Hossaert-McKey M, Anstett MC. 2003. When leaves act like flowers: how dwarf palms attract their pollinators. *Ecology Letters* 6: 28–34.

Dufaÿ M, Hossaert-McKey M, Anstett MC. 2004. Temporal and sexual variation of leaf-produced pollinator-attracting odours in the dwarf palm. *Oecologia* 139: 392–398.

Elmqvist T, Folke C, Nyström M et al. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1: 488–494.

Fedriani JM, Delibes M. 2011. Dangerous liaisons disperse the Mediterranean dwarf palm: fleshy-pulp defensive role against seed predators. *Ecology* 92: 304-315.

García Y, Castellanos MC, Pausas JG. 2016. Fires can benefit plants by disrupting antagonistic interactions. *Oecologia* 182: 1165–1173.

Gottsberger G. 1986. Some pollination strategies in neotropical savannas and forests. *Plant Systematics and Evolution* 152: 29–45.

Grundel R, Jean RP, Frohnapple KJ, Glowacki GA, Scott PE, Pavlovic NB. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications* 20: 1678–92.

Hallett AC, Mitchell RJ, Chamberlain ER, Karron JD. 2017. Pollination success following loss of a frequent pollinator: the role of compensatory visitation by other effective pollinators. *AoB Plants* 9: plx020

Harrison XA. 2015. A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. *PeerJ* 3: e1114.

He T, Pausas JG, Belcher CM, Schwilk DW, Lamont BB. 2012. Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. *New Phytologist* 194: 751–9.

Henderson A. 1986. A review of pollination studies in the Palmae. *The Botanical Review* 52: 221–259.

Herrera J. 1989. On the reproductive biology of the dwarf palm, *Chamaerops humilis* in southern Spain. *Principes* 33: 27–32.

Herrera CM, Pellmyr O. 2002. *Plant animal interactions: an evolutionary approach.* Oxford: Blackwell Science.

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. Biometrical journal. *Biometrical Journal* 50: 346–63.

Ives AR, Gross K, Klug JL. 1999. Stability and variability in competitive communities. *Science* 286: 542–4.

Jácome-Flores ME. 2015. Patrones espaciales de una palmera endémica del mediterráneo y sus efectos sobre la polinización y dispersión de semillas. PhD thesis. Universidad Pablo de Olavide, Seville, Spain.

Jácome-Flores ME, Delibes M, Wiegand T, Fedriani JM. 2016. Spatial patterns of an endemic Mediterranean palm recolonizing old fields. *Ecology and Evolution* 6: 8556–8568.

Jácome-Flores ME, Delibes M, Wiegand T, Fedriani JM. 2018. Spatio-temporal arrangement of *Chamaerops humilis* inflorescences and occupancy patterns by its nursery pollinator, *Derelomus chamaeropis*. *Annals of Botany*. doi:10.1093/aob/mcx177

Johnson SD, Steiner KE. 2003. Specialized pollination systems in southern Africa. *South African Journal of Science* 99: 345–348.

Johnson SD. 2010. The pollination niche and its role in the diversification and maintenance of the southern African flora. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 499–516.

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* 16: 406–11.

Keeley JE, Bond, WJ, Bradstock, R A, Pausas, JG Rundel PW. 2012. *Fire in Mediterranean ecosystems: ecology, evolution and management*. Cambridge: Cambridge University Press.

Knight TM, Holt RD. 2005. Fire generates spatial gradients in herbivory: an example from a Florida sandhill ecosystem. *Ecology* 86: 587–593.

Lazarina M, Sgardelis SP, Tscheulin T, Kallimanis AS, Devalez J, Petanidou T. 2016. Bee response to fire regimes in Mediterranean pine forests: The role of nesting preference, trophic specialization, and body size. *Basic and Applied Ecology* 17: 308–320.

Lemke T, Porembski S. 2013. Variation in the reproductive performance of the *Trollius*–*Chiastocheta* mutualism at the edge of its range in north-east Germany. *Oecologia* 172: 437–447.

Moretti M, Obrist MK, Duelli P. 2004. Arthropod biodiversity after forest fires: winners and losers in the winter fire regime of the southern Alps. *Ecography* 27: 173–186.

Moretti M, Duelli P, Obrist MK. 2006. Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. *Oecologia* 149: 312–327.

Moretti M, de Bello F, Roberts SPM, Potts SG. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *The Journal of Animal Ecology* 78: 98–108.

Ne'eman G, Dafni A. 1999. Fire, bees, and seed production in a Mediterranean key species *Salvia fruticosa* Miller (Lamiaceae). *Israel Journal of Plant sciences* 47: 157–163

Ne'eman G, Dafni A, Potts SG. 2000. The effect of fire on flower visitation rate and fruit set in four core-species in east Mediterranean scrubland. *Plant Ecology* 146: 97–104.

Paula S, Arianoutsou M, Kazanis D et al. 2009. Fire-related traits for plant species of the Mediterranean Basin. *Ecology* 90: 1420–1420.

Pausas JG, Keeley JE. 2009. A burning story: the role of fire in the history of life. *BioScience* 59: 593–601.

Pausas JG, Parr CL. 2018. Towards an understanding of the evolutionary role of fire in animals. *Evolutionary Ecology* 1–13.

Pauw A. 2007. Collapse of a pollination web in small conservation areas. *Ecology* 88:1759–69.

Ponel P, Lemaire JM. 2012. Coléoptères méditerranéens inféodés à *Chamaerops humilis* L. In: *Les fous de Palmiers*, Hors Série nº1 *Chamaerops humilis*, 32–37.

Ponisio LC, Wilkin K, M'gonigle LK et al. 2016. Pyrodiversity begets plant-pollinator community diversity. *Global Change Biology* 22: 1794–1808.

Potts SG, Dafni A, Ne'eman G. 2001. Pollination of a core flowering shrub species in Mediterranean phrygana: variation in pollinator diversity, abundance and effectiveness in response to fire. *Oikos* 92: 71–80.

Potts SG, Vulliamy B, Dafni A et al. 2003. Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. *Oikos* 101: 103–112.

Quantum GIS Team. 2013. *Quantum GIS Geographic Information System*. Open Source Geospatial Foundation Project. https://www.qgis.org/

R Core Team. 2017. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/

Rasband WS. 2007. *ImageJ*. U.S. National Institute of Health, Bethesda.

Saint-Germain M, Drapeau P, Hébert C. 2004. Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. *Biological Conservation* 118: 583-592.

Schütz S, Weissbecker B, Hummel HE, Apel KH, Schmitz H, Bleckmann H. 1999. Insect antenna as a smoke detector. *Nature* 398: 298.

Stanley DA, Garratt MP, Wickens JB, Wickens VJ, Potts SG, Raine NE. 2015. Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature* 528: 548–550.

Suchan T, Beauverd M, Trim N, Alvarez N. 2015. Asymmetrical nature of the *Trollius*–*Chiastocheta* interaction: insights into the evolution of nursery pollination systems. *Ecology and Evolution* 5: 4766–4777

Thom MD, Daniels JC, Kobziar LN, Colburn JR. 2015. Can butterflies evade fire? Pupa location and heat tolerance in fire prone habitats of Florida. *PloS One* 10: e0126755.

Thomson JD, Andrews BJ, Plowright R. 1982. The effect of a foreign pollen on ovule development in *Diervilla lonicera* (Caprifoliaceae). *New Phytologist* 90: 777–783.

Traveset A, Richardson DM. 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution* 21: 208–216.

Vázquez DP, Aizen MA. 2004. Asymmetric specialization: a pervasive feature of plant–pollinator interactions. *Ecology* 85: 1251–1257.

Walker B, Kinzig A, Langridge J. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2: 95–113.

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043–1060

FIGURE LEGENDS

Fig. 1. Location of the study sites in eastern Spain (left), and the burnt (B., in black) and adjacent unburned (Unb., in green) areas sampled at each site (right). Red polygons denote the fire perimeter at each site. (C= Carcaixent, D= Dénia, T=Tivissa, X=Xàbia).

Fig. 2. *Chamaeropis humilis* fruit set (proportion of developed drupes in relation to the potential drupes) of inflorescences with different pollinator exclusion treatments (pollination exclusion, wind pollination, wind and small-insect pollination, and open control). Different letters indicate statistically significant differences among treatments (for statistic values see Supplementary Data Table S1). In all figures boxplots show the median, quartiles and range of each response variable. Outliers are represented by dark dots.

Fig. 3. Pollen loads carried by the main flower visitors of *Chamaerops humilis*; (A) the weevil *Derelomus chamaeropis* (Curculionidae) and (B) the sap beetle *Meligethinus pallidulus* (Nitidulidae). Red arrows indicate pollen grains. Scale bars= 1mm.

Fig. 4. Number of *Derelomus chamaeropis* individuals per inflorescence in each study site in uburned and burnt areas for 3 postfire ages. Asterisks indicate a significant decrease of *Derelomus* individuals at the burnt area at that study site. *P* values are denoted *** $P < 0.001$.

Fig. 5. The relationship between *Derelomus chamaeropis* weevils on *Chamaerops humilis* with the distance to the fire edge at two different postfire ages in 2017 (N=401 plants). The negative

effect of distance to the edge on the number of weevils per plant was significant only 1 year postfire (Xàbia and Carcaixent sites, blue solid line). Dark shading indicates 95% confident intervals of the mean.

Fig. 6. *Chamaerops humilis* fruit set (percentage of developed drupes in relation to total number of flowers produced, i.e. the potential drupes) at each study site in burnt and unburned areas during the two years of the study and the three postfire ages. Asterisks indicate a significant decrease of *C. humilis* fruit set at the burnt area of that study site. *P* values are denoted ** *P* <0.01 and *** *P* <0.001.

Table 1. Information on the study sites.

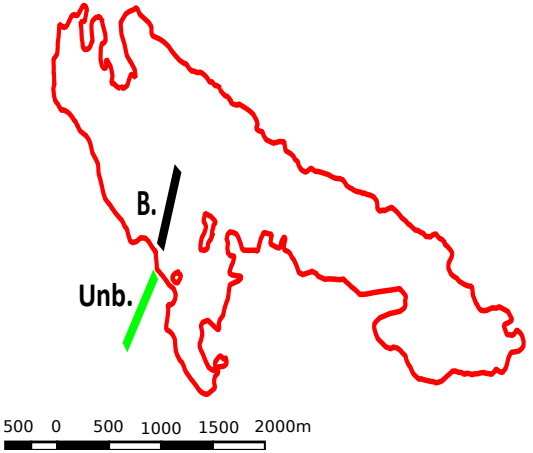
Sites	Province	Latitude	Longitude	Fire date	Sampling year	Fire ages	Burnt area (ha)
Dénia	Alacant	38.808054	0.160267	Sept. 2014	2016, 2017	2, 3	445
Tivissa	Tarragona	40.979691	0.693141	June 2014	2016, 2017	2, 3	890
Xàbia	Alacant	38.731141	0.169339	Sept. 2016	2017	1	800
Carcaixent	València	39.105267	-0.400584	June 2016	2017	1	2000

Table 2. Effects of fire (Unburned vs Burnt areas) and distance (to the fire edge) on the number of *Derelomus chamaeropis* weevils, *Meligethinus pallidulus* beetles, and *Chamaerops humilis* fruit set. For each response variable, the table shows the results of the GLM and GLMM models on the effects of fire or distance inside the fire.

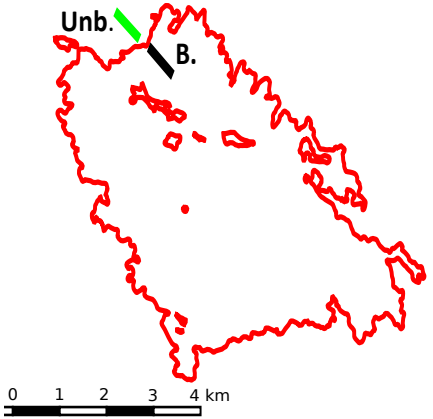
Sampling year	Response	Model	Predictor variables					
			U. vs B.	Distance	Inflorescences	Site	Plant sex	U. x Site vs B. x Site.
2016	*D. chamaeropis*	Fire	**	-	***	** [T]	***	***
		Distance	-	ns	*	** [T]	***	-
2016	*M. pallidulus*	Fire	ns	-	ns	***[T]	***	ns
		Distance	-	ns	ns	**[T]	***	-
2016	Fruit set	Fire	ns	-	ns	ns	-	**[T]
		Distance	-	ns	ns	ns	-	-
2017	*D. chamaeropis*	Fire	ns	-	*	***[X], **[C]	***	***[T], ***[X], ***[C]
		Distance	-	***	ns	***[X], ***[C]	***	-
2017	*M. pallidulus*	Fire	ns	-	**	ns	***	ns
		Distance	-	ns	*	ns	***	-
2017	Fruit set	Fire	ns	-	ns	***[T], ***[X]	-	***[X]
		Distance	-	ns	ns	***[T],***[X], *[C]	-	-

Full models for fire effects included the two way interaction ("x") between fire treatment (U. vs B. = Unburned vs Burnt) and study site. All models included the number of inflorescences, site and plant sex (only for models on *D. chamaeropis* and *M. pallidulus* abundances) as predictor variables. Names in brackets represent the study site with statistically significant effects (T= Tivissa, X= Xàbia, C= Carcaixent). * P <0.05, ** P <0.01, *** P <0.001, ns= non-significant. For detailed statistics see Supplementary data, Tables S2 (year 2016) and S3 (year 2017) and Table S4 for Post-hoc pairwise comparisons of the interaction between fire treatment and study site.

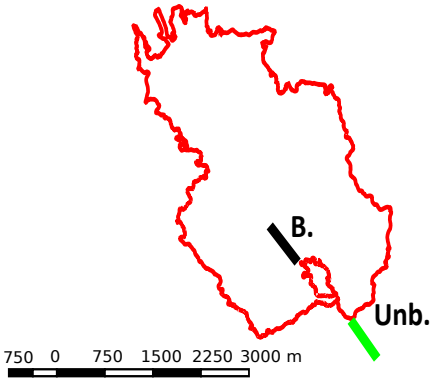
DÉNIA



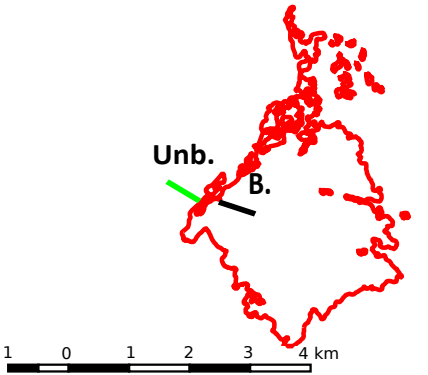
CARCAIXENT

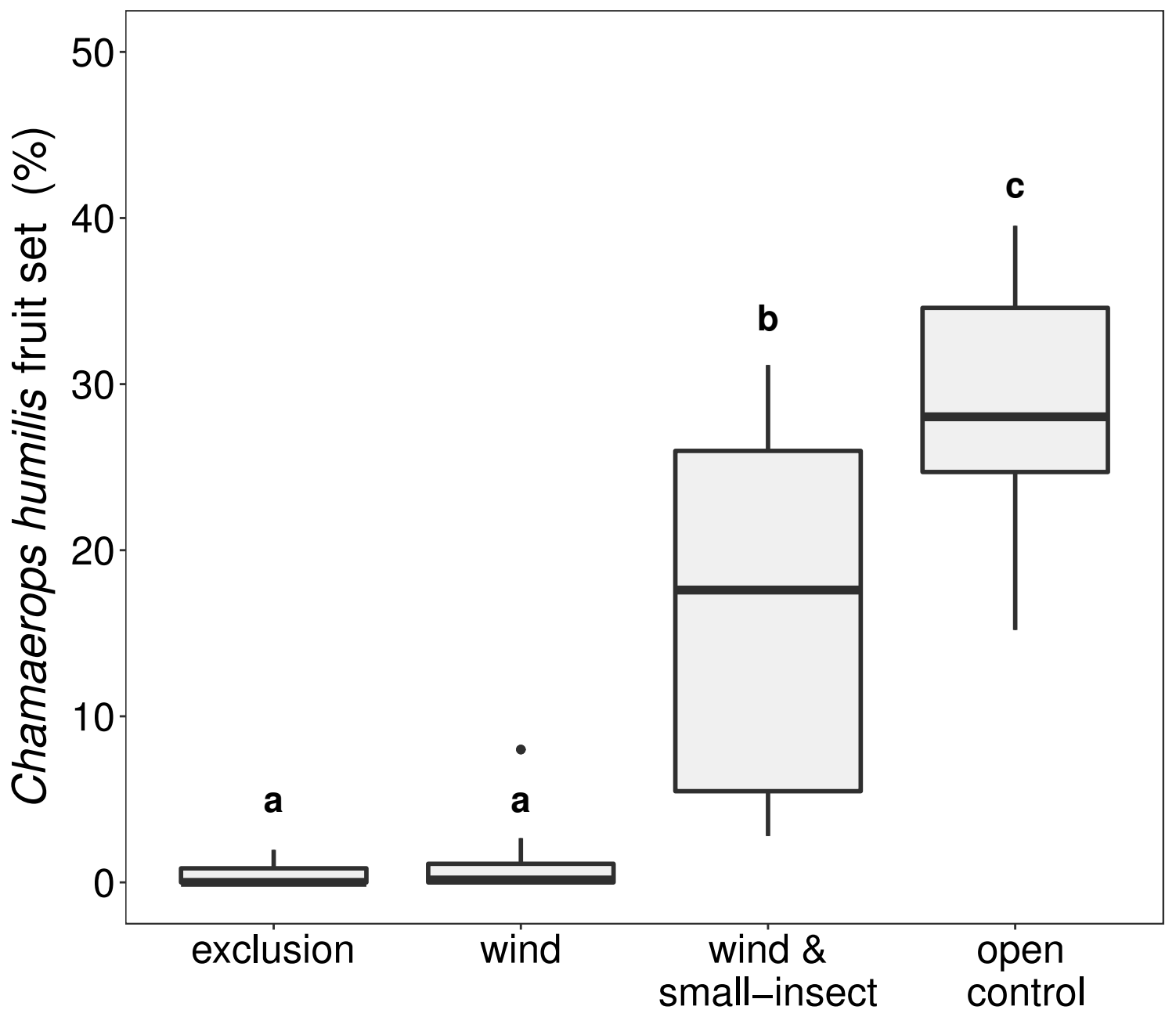


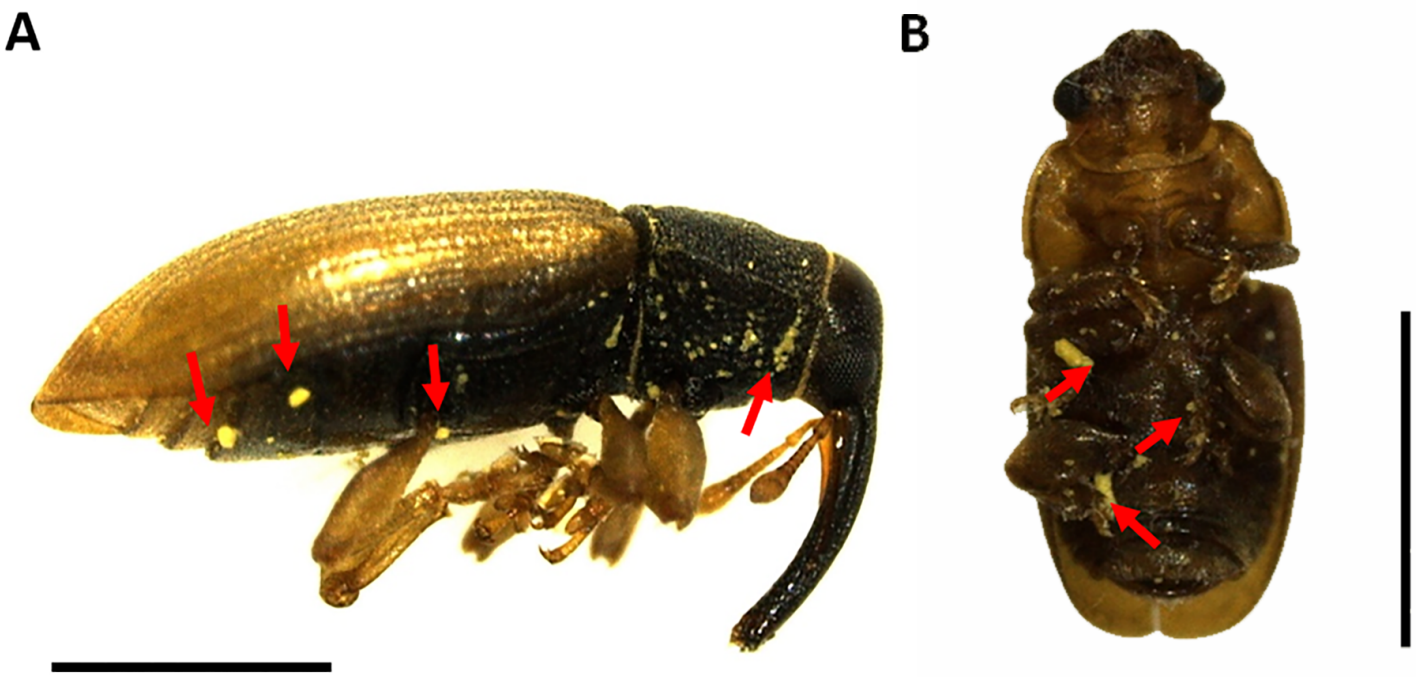
TIVISSA

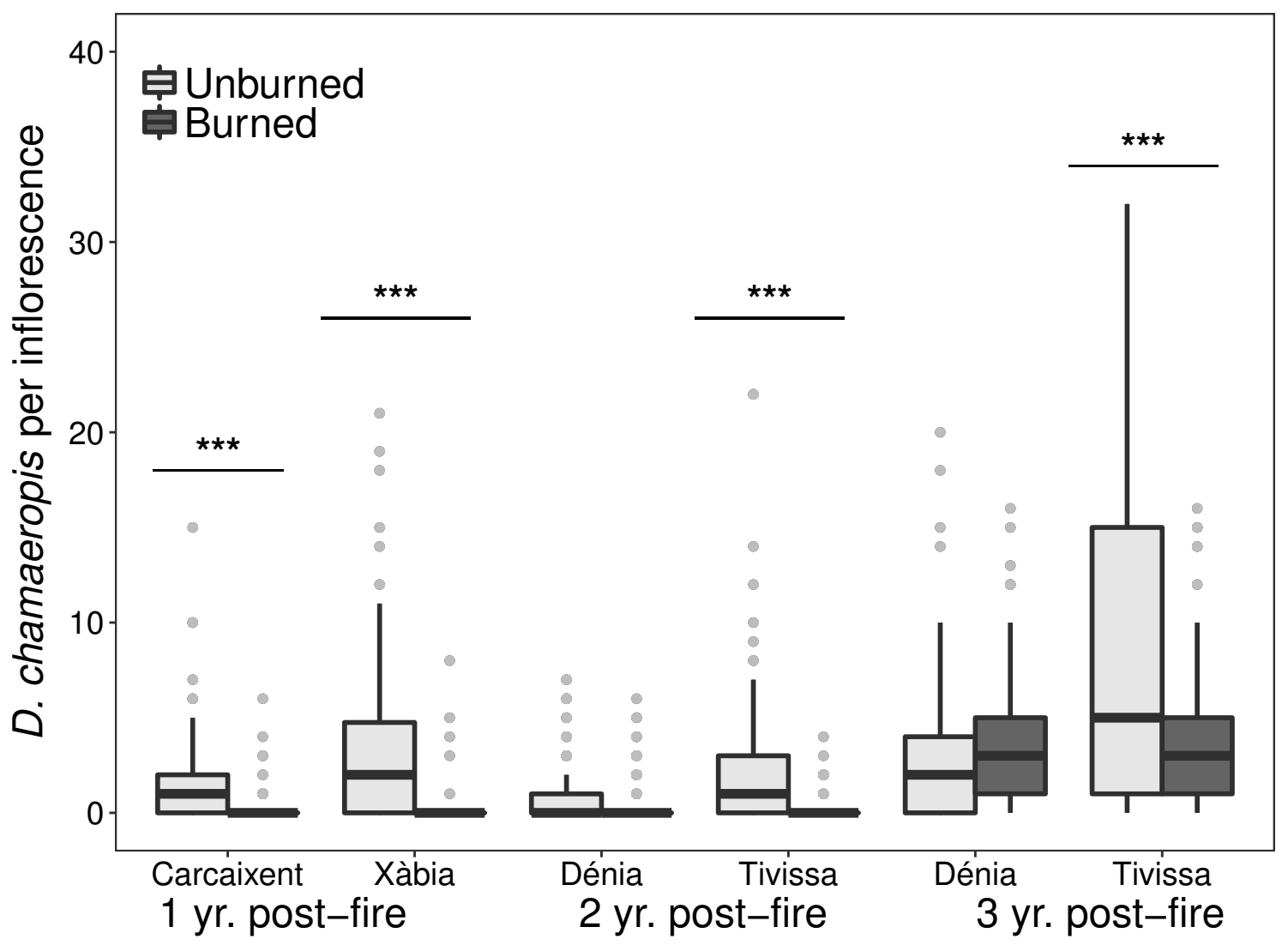


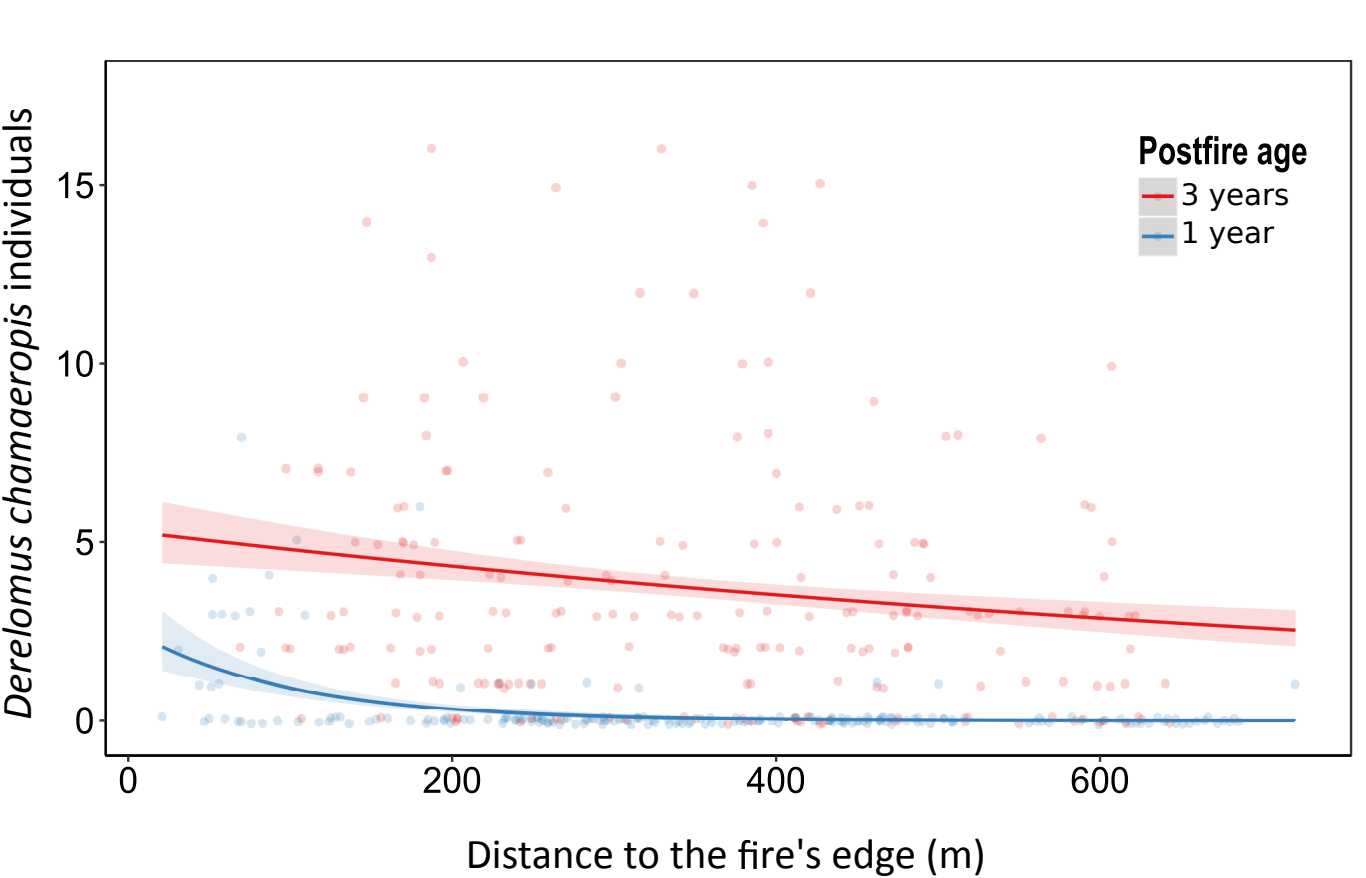
XÀBIA

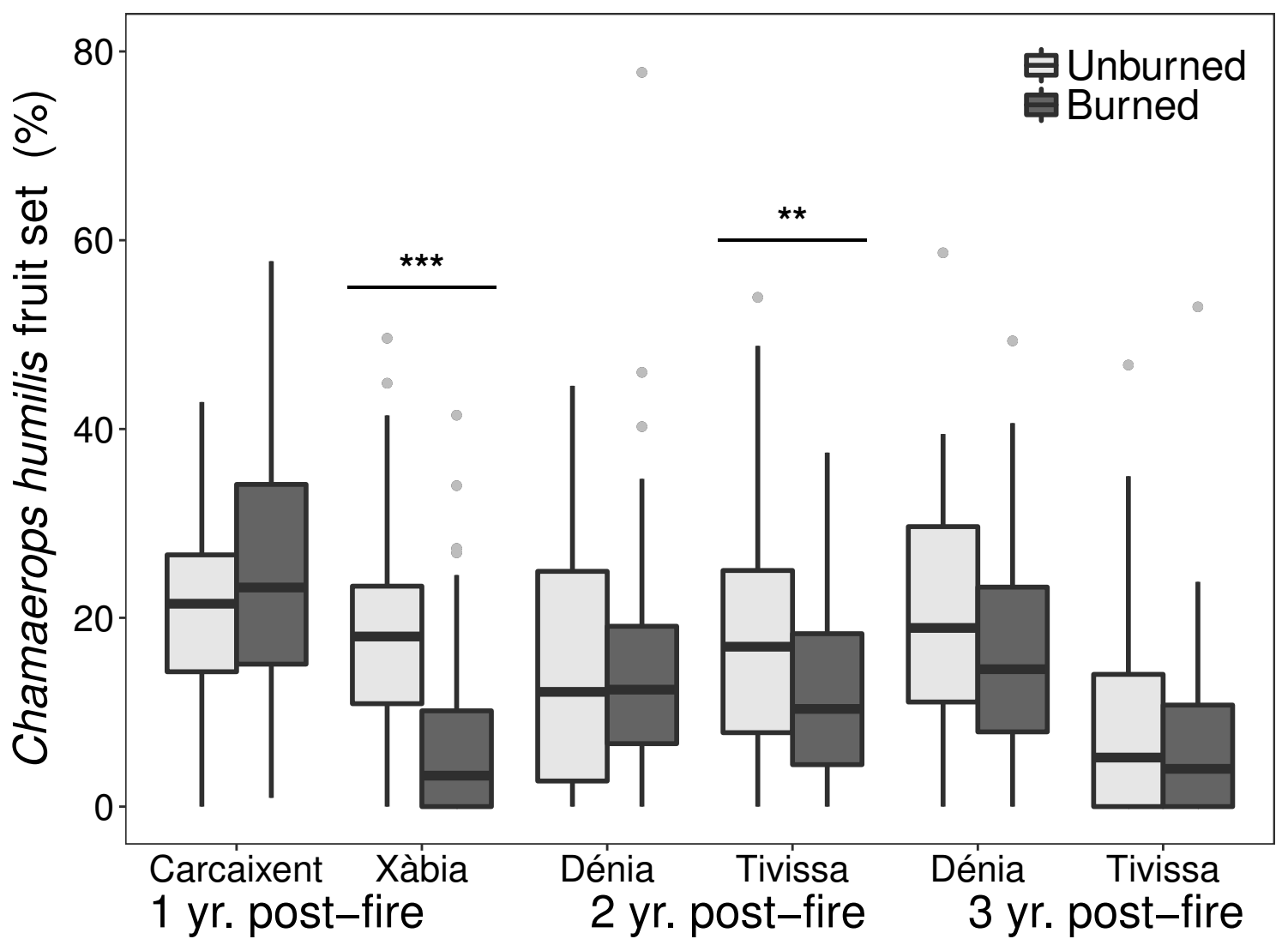



Chamaerops humilis fruit set (%)
50
40
30
20
10
0
a
a
b
c
exclusion
wind
wind & small–insect
open control


A
B


Unburned
Burned
D. chamaeropis per inflorescence
40
30
20
10
0
***
***
***
***
Carcaixent
Xàbia
Dénia
Tivissa
Dénia
Tivissa
1 yr. post−fire
2 yr. post−fire
3 yr. post−fire


Postfire age
3 years
1 year
Derelomus chamaeropis individuals
0
5
10
15
0
200
400
600
Distance to the fire's edge (m)


Chamaerops humilis fruit set (%)
80
60
40
20
0
Unburned
Burned
***
**
Carcaixent
Xàbia
Dénia
Tivissa
Dénia
Tivissa
1 yr. post–fire
2 yr. post–fire
3 yr. post–fire